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THE ADDRESS OF THE PRESIDENT

THE CHROMOSOME AND THE ORIGIN OF SPECIES

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In Lamark's Philosophy of Zoology published in 1809 and devoted to the author's views on the origin of species there is the following statement: The most important of the laws, methods, and progress of nature have nearly always sprung from the examination of the smallest objects which she contains and from apparently the most insignificant enquiries. The studies of chromosomes, nuclear bodies so minute that they escaped discovery until recently but now considered the primum mobile of nearly all life processes, have well verified the truth of Lamark's statement. That the chromosomes, insignificant in sizes as they are, constitute the only material connection between parents and offspring, and between successive generations is now common information. Also that plants and animals in general are double or as it is termed diploid, in their chromosome constitution, inheriting one set of chromosomes from their mother and one from their father parent, is well known.

The chromosome, known only since 1873, has now come to occupy a place in the front row among the biological subjects of greatest interest.

The concept of species or some comparable unit of classification must be as old as man's thinking machinery. Classification is fundamental to man's thinking and communicating about the objects of his environment. In recent years the cytogeneticists, geneticists, ecologists, and other species of biologists have gotten hold of the species concept and it has been considerably kicked around, but all have in mind the same concrete entities, plant and animal life.

Since some system of classification and designation of the classes is indispensable to man's thinking and communicating about plants and animals, which are the basis of our subsistence, anything pertaining to species concerns us all. Furthermore we are all interested in anything that can enlighten us on heredity. The taxonomists, have no reason for an inferior complex over the value of their contributions. Without a system of classification and nomenclature, the plant and animal worlds would be like large cities with no streets named or houses numbered or no other designations available for finding one's way around. Some system of classification and nomenclature is indispensable to our biological pursuits and mills of research with their grists of contributions of inestimable value.

Species are the primary units of classification as we all know. They are the entities, the concrete embodiments of the structural and functional characteristics upon which systems of classifications are founded. As defined by Linneus two centuries ago, species are groups of plants or animals distinguishable from other groups by certain observable characteristics and by the inability to cross with other groups and produce fertile hybrids. Previous to the time of Darwin and other evolutionists, the idea prevailed that species were moulded and ordered by the creator to maintain their discreteness. The acceptance of the theory of evolution was the first break in the static concept of species. With the acceptance of that theory it was necessary to accept a dynamic view of species and that the plants and animals now in existence represent only the end branches of a great tree most of which has disappeared and that any perfect system of classification should be genealogical.

Systems of classification until recently have confined their considerations largely to external characteristics, mainly of a morphological nature. It is only since 1900 that the consideration of the chromosomes has worked its way into recognition of importance in determining species. It is this broadening of the view of species to include the present appreciation of the rôle of their chromosome constitution that is the aim of this paper. In other words, the aim in this discussion is to emphasize the discovery that the creator of species is not in the heavens but in the nuclei of plants and animals.

The Rise of the Chromosome into Prominence

Although previous to 1900 there was little realization of the rôle of chromosomes in heredity and in determining the external characteristics of species, however, it had been discovered that chromosomes are definite organs of the nucleus and behave in a definite way during cell division. The biologists of last century discovered the nuclear fusion in fertilization, which brings together in the offspring a mother and father set of chromosomes. They contributed a fair account of vegetative or somatic mitosis, reporting the division of the chromosomes into lengthwise equal halves or chromatids, and the segregation of the chromatids into different daughter cells, — information necessary later in accounting for the uniform distribution of the character-determining factors in multicellular organisms. They contributed an account of reduction division and its relation to the formation of sex cells, describing the pairing of the chromosomes and the segregation of the members of the pairs into separate cells and the resulting reduction to the half number — information requisite to an understanding of the segregation and the subsequent bringing together in the offspring various associations of genes by syngamy. These discoveries paved the way for the reception of Mendelism, rediscovered in 1900, and the intensive studies of this century which have elevated the chromosomes to their present place of prominence.

In 1901, the year after Mendelism was rediscovered, Montgomery brought together almost all the cytological data necessary for its explanation. He called attention to the constant size differences of chromosomes, to the presence in pairs of the paternal and maternal chromosomes in diploid nuclei, and to the pairing and disjunction of homologous paternal and maternal chromosomes in the reduction division. Immediately following (1902, 1903) Sutton put forth with more emphasis and clarity the cytological explanation of Mendelian inheritance. These early contributions of this century emphasizing the vital relationship between heredity and chromosome behavior gave impetus to chromosome studies that grew with amazing rapidity, soon becoming world wide in their scope, enrolling a host of investigators including cytologists, cytogeneticists, geneticists, chemists, and various other scientists and resulting in a wealth of literature beyond one's ability to keep abreast. With the improved laboratory equipment and the many notable improvements in laboratory and field technique introduced during this century these investigators have made contributions that have not only greatly enriched our understanding of chromosome structure and behavior of plants and animals in general, but are of inestimable practical value in plant and animal breeding.

These researches have shown beyond doubt that the characters delimiting species and characters in general are the manifestations of particulate entities, called genes by the geneticists, that have definite locations or loci in the chromosomes. The loss or addition of genes therefore to the chromosome constitution of a species necessarily is accompanied by some disturbance in its characters. Even shifts of genes from their regular position in the chromosomes are expected to be reflected in the offspring of the individual plants or animals in which the shifts have occurred.

According to the present conception chromosomes are unquestionably continuous definitely organized bodies, provided they do not change too fast or two much. In general they are constant in number in each species, provided the species does not contain polyphoid races. They are characterized individually by definite shapes, sizes, number and location of constrictions, and in some cases by knobs or other types of appendages. Their fundamental structure is a matrix constricted at the spindle attachment and supporting within a core of thread-like structures, chromonemata in which the genes are located in linear arrangement.

The intensive study of the chomosomes throughout the somatic and reduction divisions by the cytologists and cytogeneticists in this century have not only well accounted for the parallelism between chromosome behavior and Mendelian heredity, including linkages and cross-overs, but they have gone much farther. They have revealed a number of aberrant chromosome behaviors and are rapidly accumulating evidence that these aberrancies have important genetical consequences. The chromosomes are not so stable as they were once thought to be. In addition to the frequent exchange of segments between chromatids in the cross-overs during synapsis in the reduction division, there occur apparently spontaneously the fragmenting of chromosomes, failure of chromosomes to disjoin in the reduction division or of the chromatids to disjoin in somatic cell division, the breaking away of a segment from one chromosome which may be lost or become attached to another chromosome, reciprocal exchange of sections between two chromosomes, inversions of sections of chromosomes, and incomplete cell divisions in which the chromosomes that should go to the two daughter nuclei are incorporated in a single restitution nucleus. As a result of these pranks the chromosomes of complements are variously changed not only in size and number, but in the association and orientation of the genes. When these modified chromosomes or new chromosomes, if formed, are segregated in reduction division and are brought into associations in various ways with other modified, new and normal chromosomes in fertilization, they may be the cause of many variations in offspring that perpetuate as new types. In case of increase in the number of chromosomes of complements as results from non-disjunctions in cell divisions and the doubling of the number in restitution nuclei, offspring that may be perpetuated as new races or new species with a larger number of chromosomes and new characteristics may arise. Now there are good reasons for believing that the effects of these aberrations and others not mentioned, in combination and in combination with gene modifications that are associated as yet with no observable chromosome modifications, play a considerable rôle in the origin of species.

The case in which the chomosome number of the complement is doubled affords probably the most apparent illustration of the bearing of aberrations on the origin of new species, and also the practical applications they may have in improving our cultivated plants.

Polyploidy (Amphidiploidy) and its Relation to Species Formation

The doubling of the number of chromosomes of a complement including both parental sets is commonly called tetraploidy or amphidiploidy. There are two types of tetraploids or amphidiploids, one known as autotetraploids in which the two parental sets of the chromosome complements doubled are alike, and the other, allotetraploids, in which the chromosome sets are unlike, as in the case of hybrids. The number of times they have arisen in experimental plots and the many known cases in which races within species and species within genera differ in chromosome numbers by some basic chromosome number afford convincing evidence that tetraploidy has been a prevalent process in plants. In animals, however, although the species of genera may differ in chromosome number, the evidence of the doubling of either one or both parental chromosome sets is much less than it is in plants, the explanation being that the sex mechanism in most animals is not favorable to the polyploid origin of species. The alteration in chromosome numbers in animals must come about in a less wholesale manner.

The difference in chromosome numbers in species of wheat by a basic number 7, in species of chrysanthemum by a basic number 9, and in species of Solanum by a basic number 12 are familiar examples of polyploidy in genera. It is thought that half or more of the Angio sperms are polyploids, but polyploidy is also prevalent in the lower plants. The fact that a survey of the chromosome numbers in more than 2000 species of plants shows that the even numbers are much more frequent than the odd numbers is further evidence that polyploidy has played a considerable rôle in the evolution of species.

The origin within species of individuals with double the normal number of chromosomes (autotetraploidy) has apparently repeatedly occurred spontaneously in many groups of plants. It has been induced a number of times experimentally. In his discussion of autopoloploidy, Muntzing (7) describes 58 cases of intraspecific polyploids which are evidently autotetraploids that have been discovered and 11 that have been produced experimentally. Since his publication in 1936 others have been recognized and autotetraploids have been produced experimentally in barley, wheat, oats, rye, and sweet clover.

The results of autopoloploidy, whether occurring naturally or induced experimentally, are very similar. In contrast to the diploid races, autotetraploids are less fertile within themselves and also with the diploid races. They tend to be larger and incline toward the perennial habit. They commonly surpass the diploids in resistance to drought, cold, and heat and in adaptability to different habitats. In some genera, as for example in plants of the Crepis genus, autotetraploids forms of existing species are common and a number of distinct Crepis species are known which apparently arose through autotetraploidy.

In allotetraploidy, where it is a matter of the doubling of the chromosomes in hybrids, the results are more striking than in autoteraploidy, owing to the fact that the parental sets of chromosomes doubled are unlike. One of the notable features of allotetraploids is their fertility which surmounts the difficulty of the sterility of the hybrids from which they arise. By transforming hybrids, which are characteristically sterile, into allotetraploids which are generally fertile, the combinations of characters in the hybrids can be perpetuated.

Winge (8) in 1932 listed 24 known cases in which fertile and constant hybrid species have arisen through a doubling of the chromosome numbers of hybrids. Some have been discovered and some produced experimentally since that date. In the grass family generic allotetraploid hybrids between wheat and rye, wheat and Aegolops, and wheat and Agropyron have recently appeared.

The number of allopolyploid hybrids that have appeared in experimental plots suggests their common occurrence through the past. One of the earliest recorded is the *Primula Kewensis* which arose in 1900 from a cross of *P. floribunda* and *P. verticillata*. This species is fully fertile and has long been in cultivation. The *Primula Aileen* Aroon in cultivation has been demonstrated to be of similar origin. The origin of a constant fertile allotetraploid turnip from a cross of the Swedish and common turnip: the radish-cabbage hybrid produced by Karpechenko by crossing the radish and cabbage; two alloteraploid tobaccos arising from crosses of diploid species of tobacco; an allotetraploid strawberry from a cross between *Fragaria bracteata* and *F. Helleri*; a constant hybrid from a cross of two diploid species of Saxifrage; a new constant form of columbine from a cross between two diploid Aquilegia species; an artificial species tetrahit in the genus Galiopsis by crossing two diploid species of this genus and in the grass family the amphidiploid forms arising from crosses of wheat with rye, of wheat with Agropyron, wheat with Aegelops, Euchlaena with Zea, and those arising from crosses between species of Bromus, and Festuca, all arose on experimental plots and spontaneously insofar as the doubling of the chromosomes was concerned. Among those whose history is more obscure but afford pretty definite evidence of allotetraploid origin is the cultivated tobacco, apparently an allotetraploid which arose from a cross of two diploid forms of the tomentosa and sylvestris types. It is an illustration of what allopolyploidy can do toward the improving of crop plants.

It is of interest to note further the ways in which allopolyploids differ from the diploid species. Their tendency toward gigantism is a general characteristic. They grow more slowly as a rule but continue their growth longer and thus tend toward the perennial habit. They are more variable, more adaptable to environment, usually have a wider range, and can endure harder conditions, and in some cases have been proven to be and probably most of them are more resistant to diseases.

The greater range of allotetraploids is illustrated by the following cases. In the Tradescantia, as reported by Anderson, the range of the diploids is limited to a relatively small area stretching from northern Texas to Arkansas, whereas the tetraploid forms have spread out over the plains and Mississippi valley. Studies of the cacti reveal that in general those with the highest chromosome number have the widest distribution. In contrast to the diploids, Hagerup (5) states that the tetraploid orchid, *Orchis maculatus*, has a wider geographical distribution, a greater abundance of individuals, a greater capacity to tolerate dryness, moisture, cold, and acidity of the soil. The cases demonstrating the tendency toward the perennial habit are many. In the sorghums the diploids are annual while the Johnson grass, a perennial propagating by rootstocks, is a perennial. The autotetraploid of *Euchlaena mexicana*, an annual, and of Zea, are perennial. In Eragrostis the species with low chromosome numbers are annual, while the polyploids are perennial. In a study of 582 species distributed among nearly 50 different genera, representing widely separated families, Muntzing found the odds 57 to 1 that the perennial species in his material have higher chromosome numbers than the biennials and annuals, the average chromosome number of the annuals being 10 and that of the perennials 15 and 16.

In resistance to cold polyploids are often much more hardy than diploids. A positive correlation between chromosome number and hardiness is illustrated by the tetraploids of the hybrid oats produced from a cross of *Avena barbata* and *A. strigosa*. Among the 26 species and varieties of arctic grasses from Spitzenberg, Flovik found only one diploid and other studies of 70 species and varieties of flowering plants from the high arctic islands show that 80 per cent of them are polyploid, confirming the conclusions of Hagerup and Tischler that in unfavorable climates a higher percentage of polyploids will be found than in climatically favorable regions.

It is probable that chemically polyploids differ quite generally from diploids, one case already known being the greater vitamin C content in polyploid tomatoes and pomaceous fruits in contrast to diploids.

Through tetraploidy a number of plants of greater economic value than the diploid species of the genus have arisen. One notable example is the *Spartina townsendii*, a tetraploid of a hybrid between two other Spartina species and found especially adapted to salt marsh meadows of the European shores. Another is a wheat-agropyron tetraploid hybrid recently produced and combining the drought resistance and the perennial habit of the Agropyrons and the grain production of the wheat, a plant desirable for both grain and hay. I may mention that in contrast to the Asiatic cottons the American cottons are tetraploids.

In 1926 Muller showed that by X-rays chromosomes could be induced to mutate in the species of Drosophila, duplicating the aberrations just described. In 1932 Randolph produced a tetraploid in Zea by a heat treatment. More recently tetraploidy has been induced in barley, wheat, rye, and the biennial sweet clover by the heat treatment. Chemicals, especially colchinine is now being used with considerable success in inducing the doubling of chromosomes. By applying a solution of colchinine to growing tips of flax an autotetraploid has been obtained and by a similar treatment of the growing tips of a hybrid between the black and white henbane a number of allotetraploids has been induced. Blakeslee reports that at Cold Spring Harbor 65 different kinds of flowering plants, representing 41 species, 24 genera and 14 families have been induced to double their chromosomes by the colchinine treatment. By the application of the artificial methods it is apparently possible to duplicate many if not all of the mutations that appear spontaneously in nature and on the experimental plots. Of course these artificial methods are still unrefined, the experimenter having practically no control over their results, but they do open up a field in which much may be accomplished in the future in improving our cultivated plants. Greater resistance to drought, heat, cold, and diseases, a wider range of adaptability, longer lived, greater vegetative yields and increased seed production, the characteristics that tetraploids commonly have in contrast to diploids, are the improvements in demand in many of our cultivated plants. For example, in the grass family, where there are so many economic species and races, there are 150 or more hybrids known of which many if not most of them would be greatly improved in seed production, in length of life, resistance to drought, heat, and cold, and in greater range of adaptability by tetraploidy. The same applies to many of the legumes and other cultivated crops in general. The extent of the practical applications of tetraploidy and the other aberrations may compete with Mendelsim in importance. It may be possible in a few years to produce about and type of plant we want by chromosome manipulations.

Summary

The sum and total of the chromosome investigations have gone far toward making biologists and those in fields related to biology chromosome minded, as some recent statements show. Sirk with a cytogenetic viewpoint states that a similarity in chromosome number and form and regularity in meiosis in intra-crosses should be determining characteristics of species. Anderson, a taxonomist, says that cytology is unique in that it may indicate not only a difference between species but may also show the way in which the differences came about. Recently Clausen (2) with an ecological squint and cenospecies and ecospecies well established in his vocabulary says that in addition to the common taxonomic characteristic and physiological and ecological reactions, the chromosome constitution should be considered in determining species. Even the physicists think of genes when they look through their super microscopes and the chemists wonder about them. Species have lost some of their mysteriousness. They are producible experimentally and appear spontaneously within our fields of observation. There is a rapidly growing appreciation of the importance of the aberrant chromosome behaviors in the origin of species and in their practical applications in plant improvements.

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